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Breaking the symmetry between interaction and replacement in evolutionary dynamics on graphs

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We study evolutionary dynamics in a population whose structure is defined in terms of two graphs: the interaction graph determines who plays with whom in an evolutionary game; the replacement graph specifies the structure of evolutionary competition. We investigate the evolution of cooperation modeled in terms of social dilemmas associated with symmetric 2×2 games played in finite populations and show that it is always harder for cooperators to evolve whenever the interaction graph and the replacement graph do not coincide. In the thermodynamic limit, we show that the dynamics taking place on both graphs is given by a replicator equation with a rescaled payoff matrix in a rescaled time, a result which is valid for general symmetric $m \times m$ games with $m \geq 2$. Our analytical results are obtained using the pair-approximation method in the limit of weak selection, whose validity is checked by exact computer simulations.

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The recent availability and systematic characterization of empirical data specifying the networks of contacts between individuals of a given community or population [1, 2] has spurred a renewed interest in the study of dynamical processes in structured populations [1–16]. In this context, investigation of evolutionary game dynamics constitutes a very appealing and widely used framework, from *physics* to *political science* [1–16]. The traditional approach to evolutionary game dynamics involves the replicator equation, which describes deterministic dynamics in infinitely large populations [17]. When populations are finite, the impact of stochastic effects should not be overlooked [18, 19], and many novel insights have been gained recently by bridging the gaps between stochastic and deterministic dynamics and between finite and infinite populations [20, 21]. In particular, the study of stochastic dynamics in finite populations has received a lot of attention (for a review, see [15]).

However, population structure is often more complex than that emerging from a single static graph description[1]. Indeed, individuals do not usually rely on a single network to carry out their decisions, (strategic) decision making being often based on additional information about the interacting partner, obtained via (gossip, rumor, etc.) networks which rarely overlap perfectly with the network of interactions. Similarly, seldom our role models are those we have the possibility to interact with regularly. Finally, our network of close friends often bears little resemblance with the network of our professional relations, similarly to what one observes in the animal world, where grooming and other manifestations of close relationship are usually established among kin, despite the fact that often fitness is acquired via interaction with the non-kin. Hence, consideration of dynamical processes in more than a single network constitutes an important ingredient which has been ignored so-far, and which may be of relevance to other processes such as rumor spreading, traffic regulation, and epi-

demic modeling, to name a few. In this work we explore a first step toward the inclusion of these more sophisticated layers of population structure, by explicitly distinguishing two types of graphs defining the networks of contacts between individuals: the interaction graph, H , determines who-meets-whom in an evolutionary game; the replacement graph, G , specifies evolutionary updating or, in a social context of cultural evolution, the network defining who-is-the-role-model-of-whom. Both graphs have the same vertices, where each vertex is occupied by one individual, with no empty vertices. The graphs H and G may differ in their edges, however. Hence we break the symmetry between these two types of graphs, compared to the more traditional approach, in which the two graphs coincide. This simple model allows us to explore the new features associated with this richer and more powerful representation of population structure, and also allows us to derive approximate analytical results whose validity is assessed by means of computer simulations. It will be concluded that, whenever the symmetry between graphs H and G is broken, it is harder for cooperators to thrive compared to the case when the two graphs coincide. More realistic implementations should also take into account that strategies and structure co-evolve with variable time-scales [22, 23], a feature which may preclude the derivation of explicit analytical results, such as those derived here.

Let us consider social dilemmas associated with symmetric 2×2 games with two pure strategies, cooperators C and defectors D , with associated payoff matrix Φ whose entries represent the payoffs for the row player:

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \quad (1)$$

R is the reward for mutual cooperation, P is the punishment for mutual defection, T is the temptation to defect, and S is

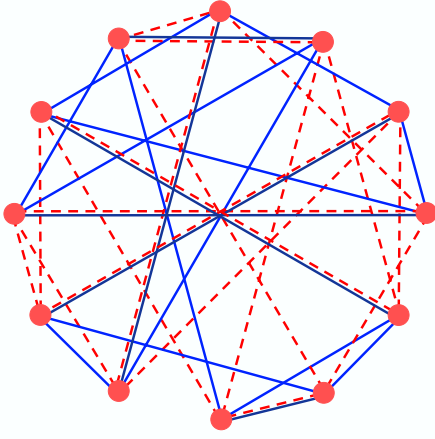


FIG. 1: (color online) Solid blue lines belong to the interaction graph H , with connectivity h ; dashed red lines belong to the replacement graph G , with connectivity g ; double lines (dashed red and solid blue) define the overlap graph L , with connectivity l . In the example shown, all graphs are random and homogeneous [31]. The procedure to generate them is straightforward: given values of h, g, l , we start by constructing a random regular graph [31] of degree g , ensuring that it is connected. Subsequently, we augment this graph by increasing the connectivity of all nodes by $h - l$, such that G has connectivity g , H has connectivity h and L has connectivity l .

the sucker's payoff. Different orderings of these four payoff values define three well-known social dilemmas: The prisoner's dilemma (PD) ($T > R > P > S$), the snowdrift game (SG) ($T > R > S > P$), and the stag-hunt game ($R > T > P > S$) [8].

Each individual uses either strategy C or D , which she plays with all her immediate neighbors in the interaction graph, H , accumulating a total payoff Π . The fitness is given by $F = 1 - w + w\Pi$. Here $0 \leq w \leq 1$ represents the relative contribution of the game to fitness. If $w = 1$ then the payoff is equal to fitness. This is the case of 'strong selection'. If $w = 0$ then the game is irrelevant for fitness; all players have the same fitness. This is the case of 'neutral drift'. Throughout this paper we study the limit of 'weak selection' [18], $w \ll 1$, which can be justified in different ways: First, in most real life situations we are involved in many different games [1], and each particular game only makes a small contribution to our overall performance. Second, weak selection leads to important analytic insights which are often not possible for strong selection (for an exception, see Ref. [19]). Simulations suggest, however, that these results are usually good approximations for larger values of w [9]. Whereas fitness is acquired through the interaction graph H , updating dynamics proceeds on graph G . Following Ref. [9] we adopt Death-Birth (DB) updating: A random individual is chosen to die; the g neighbors in the replacement graph compete for the empty site proportional to their fitness. Reproduction can be genetic or cultural. In general, however, different update mechanisms may be of relevance [24, 25]. Details of the present framework

and its extension to other update mechanisms and to games in infinite structured populations, involving an arbitrary (finite) number of strategies will be published elsewhere [25].

In a finite population of size N , a relevant quantity to consider is the fixation probability, defined as the probability that a mutant invading a population of $N - 1$ resident individuals will produce a lineage which takes over the whole population [18, 26, 27]. We denote the fixation probability of strategy X ($=C$ or D) in a Y -population ($=D$ or C , respectively) by ρ_X . For a neutral mutant $\rho_C = 1/N$. If $\rho_C > 1/N$, then natural selection favors the fixation of strategy C . In order to derive an analytical result for the fixation probabilities, we resort to the diffusion approximation under weak selection, e.g., $Nw \ll 1$ with $N \gg \max\{g, h\}$, where g, h and l are defined in Fig. 1.

Let x_X denote the global density of strategy X ($=C$ or D). Let T_C^+ (T_C^-) be the probability that the number of C -strategists increases (decreases) by one in each update event. The probability $\phi_C(y_C)$ that strategy C ultimately takes over the whole population, when its initial frequency is y_C , is given as the solution of the backward Kolmogorov equation [28]

$$0 = m(y) \frac{d\phi_C(y)}{dy} + \frac{v(y)}{2} \frac{d^2\phi_C(y)}{dy^2}, \quad (2)$$

where $m(x_C) = T_C^+ - T_C^-$ is the mean of the increment of x_C per unit time and $v(x_C) = (T_C^+ + T_C^-)/N$ is the variance of the increment of x_C per unit time. From this equation, the fixation probability is calculated as $\rho_C = \phi_C(1/N)$. Hence, we need to calculate T_C^+ and T_C^- .

Clearly, the state of the population can no longer be described in terms of global densities of strategies, x_C and x_D (mean-field approximation). In each particular configuration of the population, each vertex can be either occupied by an C or a D individual. There are 2^N possible configurations on a graph, a huge number for large N . Here we adopt the pair-approximation method [29, 30] in order to describe the local configurations of strategies on graphs. Pair-approximation considers not only frequencies of strategies, but also frequencies of (connected) strategy-pairs which enables us to estimate the correlation of strategies in two adjacent nodes. We have three different types of pairs: those connected only through G , those connected only through H , and those connected through both graphs. We label each of them (G) , (H) , or (L) , respectively.

Let $q_{X|Y}$ be the conditional probability that the focal node is occupied by strategy X ($=C$ or D) given that strategy Y ($=C$ or D) occupies the adjacent node. This conditional probability depends on the type of edges connecting X and Y . Therefore, we need to distinguish $q_{X|Y}^{(G)}$, $q_{X|Y}^{(H)}$, and $q_{X|Y}^{(L)}$. In the weak selection limit, we expect these 'local' conditional probabilities to equilibrate much faster than global frequencies of strategies, x_X , since the latter will equilibrate at a speed of order w . Hence, the system reaches a local steady state characterized by the following values for the local fre-

quencies, independent of the update dynamics [25]

$$q_{X|Y}^{(H)} = x_X, \quad q_{X|Y}^{(G)} = q_{X|Y}^{(L)} = \frac{g-2}{g-1}x_X + \frac{1}{g-1}\delta_{X,Y}. \quad (3)$$

The intuition behind these expressions is the following. It is obvious that correlations between two adjacent nodes build up only through G , and not via H . Hence, the local conditional probability $q_{X|Y}^{(H)}$ is given by its global frequency, x_X . Regarding the other edges, (G) and (L) , with probability $1/(g-1)$ a player shares a common ancestor with his neighbor. With the remaining probability, $(g-2)/(g-1)$, his neighbor is a random individual. With these values for the local probabilities, we can calculate T_C^+ and T_C^- . For **DB** updating the condition $\rho_C > 1/N$ leads to the equation

$$g^2h(R+2S-T-2P) > gl(2S-2R+P-T)+l(S-R-P+T) \quad (4)$$

and

$$\rho_C > \rho_D \iff (gh+l)(R-P) > (gh-l)(T-S). \quad (5)$$

Let us now apply the general results above to the two-parameter PD; a cooperator, C , pays a cost c for every edge, and the partner of this edge receives a benefit $b > c$. Defectors, D , pay no cost and distribute no benefits. Hence, $T = b$, $R = b - c$, $P = 0$ and $S = -c$. From eqs.(4) and (5) we find that that $\rho_C > 1/N > \rho_D$ if

$$\frac{b}{c} > \frac{hg}{l}. \quad (6)$$

The inequality above, which is valid for **DB** updating only [25], suggests that for fixed b and c , the optimum configuration for evolution of cooperation occurs when $h = g = l$. The degree l of the overlap should be as large as possible, while the degrees h and g should be as small as possible. This optimum is reached when the replacement graph and the interaction graph are identical. In this limit we recover our previous condition, $b/c > k$ (using $k = h = g = l$) [9]. Any deviation from the identity between the interaction and the replacement graphs makes evolution of cooperation more difficult. Note also that cooperation is never favored if the overlap between interaction and replacement graphs is empty ($l = 0$). Furthermore, the critical threshold condition (6) is symmetric in the degrees of the replacement and interaction graphs, g and h . Therefore, a highly connected replacement graph (large g) and a sparsely connected interaction graph (small h) have the same threshold as the reverse situation (for a fixed overlap l).

The results obtained, however, strongly depend on the game under study. Let us now discuss the social and biologically relevant SG[4], parameterized in terms of costs and benefits. In the SG a cooperator pays a cost c , but two cooperators share this cost. Whenever one player cooperates, both receive a benefit $b > c$. Hence, $T = b$, $R = b - c/2$, $S = b - c$ and $P = 0$. Now the condition $\rho_C > 1/N$ leads to $b/c > [5/2 - x - x/(2g)]/[2 + x - x/g]$, and becomes always easier to fulfill than $\rho_C > \rho_D$ which now reads

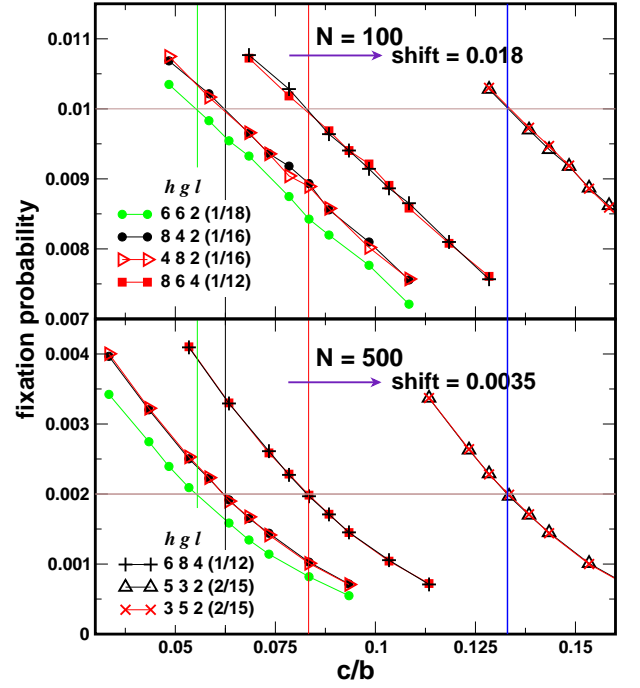


FIG. 2: (color online) Analytical versus numerical calculation of fixation probabilities. We consider populations of size $N = 100$ (upper panel) and $N = 500$ (lower panel). We generate 3×10^3 graphs G and H compatible with fixed (h, g, l) , and run 5×10^3 simulations for each graph. We compute the average fixation probability of a single cooperator in a population of defectors. $w = 0.1$ in all cases. The intersection between vertical lines and the horizontal lines at $1/N$ provide the values predicted analytically by eq.(6), given in brackets, for each triplet h, g, l . Symbols provide the results of numerical simulations. Note that all datasets have been rigidly shifted by the amounts indicated in the panels, reflecting the finite size effects which scale as $1/N$. Color and line symbols are the same in both panels.

$b/c > (3-x)/(2+2x)$, where $x = l/gh$. Similarly to the PD, selection will be more favorable to cooperators if the overlap is maximized. Unlike the PD, however, cooperators may now become advantageous even if the overlap l is zero. Furthermore, $\rho_C > 1/N$ is no longer symmetric in g and h : As a result, it is better to have more role models than interaction partners in the SG.

The pair approximation is only valid for infinite Bethe lattices (or Cayley trees) where each node has exactly the same number of links and there are no loops or leaves. However, it was found in Ref. [9] that, under weak selection, pair-approximation works extremely well for random regular graphs and other structures, despite deviations found for scale-free graphs. We shall test the validity of eq.(6) by means of numerical simulations for the PD on random regular graphs [31], which lead to population structures such as those illustrated in Fig. 1.

The results are shown in Fig. 2. An excellent agreement with the theoretical predictions is obtained. In particular, the numerical simulations confirm the invariance of the condition above upon exchange of h and g . Finite size effects account for the rigid shift of ≈ 0.018 toward lower values of c/b for $N = 100$ and of ≈ 0.0035 for $N = 500$ between the simulation results and the theoretical predictions, which suggest a $1/N$ dependence and an overall insensitivity to the specific values of g , h and l . Hence, as the population size increases, the agreement between the pair-approximation-based predictions and computer simulations improves. In practice, for a given finite value of N we need b/c to be slightly larger than the thresholds predicted by our analytical calculations.

Finally, we discuss the implications of breaking the symmetry between interaction and replacement in what concerns the thermodynamic limit. When $N \rightarrow \infty$ the description becomes deterministic, since the variance $v(y)$ goes to zero as $1/N$. Hence, the rate of change of the global frequency of cooperators x_C is given by $\dot{x}_C = T_C^+ - T_C^-$. Here we shall discuss the results for 2×2 games, although the main results remain valid for m strategies interacting via general $m \times m$ symmetric games [25], for which the replicator equation in a well-mixed population reads [13],

$$\dot{x}_i = x_i(e_i \cdot \Phi x - x \cdot \Phi x), \quad (7)$$

$i = 1, \dots, m$, where e_i is the i -th unit column vector, whereas $x = (x_1, \dots, x_m)^T$. For the general social dilemmas defined in eq.(1) and keeping only the linear terms in w in $T_C^+ - T_C^-$ (weak selection) we obtain [32]

$$\dot{x}_C = \tau x_C [e_C \cdot (\Phi + \Psi)x - x \cdot (\Phi + \Psi)x] \quad (8)$$

where the matrix Ψ reads

$$\begin{matrix} C & D \\ C & \begin{pmatrix} 0 & \sigma \\ -\sigma & 0 \end{pmatrix} \end{matrix}; \sigma = \frac{l[(g+1)R + S - T - (g+1)P]}{g^2h - (g+2)l} \quad (9)$$

and the time scale constant reads $\tau = w(g-2)(g^2h - (g+2)l)/[g^2(g-1)]$. Eq.(8) has precisely the form of a replicator equation (7) with time re-scaled by the constant τ and an effective payoff matrix given by $\Phi + \Psi$. Naturally, the matrix Ψ will depend on the update mechanism employed. However, it can be shown that this matrix is always anti-symmetric, even in the case of $m \times m$ games with $m > 2$ [25].

To summarize, breaking the symmetry between interaction and replacement graphs makes it harder for cooperation to evolve in the prisoner's dilemma in which, for cooperation to thrive, it is important that our interaction partners are also our role models. By studying the limit of weak selection, and making use of the pair approximation, we were able to provide simple conditions under which a cooperator becomes advantageous when immersed in a population of defectors. Comparison with exact computer simulations shows that, apart from population size effects, which scale as $1/N$, the analytical conditions fit nicely the numerical results.

In infinite, structured populations, and in the limit of weak selection, strategies evolve according to a replicator equation. The effect of population structure is now to induce a transformation of the payoff matrix which affects solely its off-diagonal elements. Once such a transformation is performed, then evolution proceeds "as if" the population were well-mixed (unstructured).

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